



# New insights on the role of the holoplanktonic mollusk *Firoloida desmarestia* (Gastropoda: Pterotracheidae) as host for digenetic trematodes

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## Abstract

Interactions of holoplanktonic mollusks with symbionts and parasites are poorly known. We investigated the ecology of infection (prevalence, intensity, and abundance) in *Firoloida desmarestia*, caught during two sampling campaign sessions in 2012, off the Baja California Peninsula, Mexico (IMECOCAL, 83 stations) and a coastal research center near La Sorpresa Beach, Baja California Sur, in the Gulf of California (14 stations). Only females of *F. desmarestia* were parasitized. Hemiuroidea parthenita rediae infected 1% of *F. desmarestia* population at IMECOCAL, whereas young unencysted metacercariae stages of *Opechona pyriformis* (Lepocreadiidae) parasitized 6.6% of the same host species at La Sorpresa. Overall, finding of rediae and metacercariae represent new geographical and host records and shows that *F. desmarestia* has a dual host function in the life cycle of trematodes. As first intermediate host, *F. desmarestia* harbors hemiuroid rediae, functioning as the source of infection to other zooplanktonic groups by dispersing successive cercariae. As second intermediate hosts, it harbors infective unencysted metacercariae stages of *O. pyriformis*, which parasitize nektonic predators (fish), most likely through trophic interaction. Our results suggest that some trematodes are able to spend their entire life cycle infecting only pelagic hosts. Parasite–*F. desmarestia* interaction is shown in a conceptual model, where we propose that transmission of trematodes may occur between individuals of *F. desmarestia* within the same swarm. Relevance of *F. desmarestia* as a potential host in which life cycle abbreviation of trematodes may take place is discussed. This is the first quantitative study of helminth interaction on *F. desmarestia* in the Eastern Pacific.

**Keywords** Hemiuroidea redia · Metacercaria · *Opechona pyriformis* · *Firoloida desmarestia* · Symbionts · Dual host function

## Introduction

Development of digeneans includes parthenogenetic and hermaphroditic generations, as well as two free-living dispersive

stages. This parasite group successfully exploits several species from different trophic levels used as paratenic, intermediate, or definitive hosts to accomplish their life cycles, while in other several trematode taxa, the life cycle is truncated (Poulin and Cribb 2002; Parker et al. 2003; Niewiadomska and Pojmanska 2011; Zimmermann et al. 2016). Excepting some members of the family, Aporocotylidae, the host–digenea interaction model typically integrates benthic or neritic mollusks, functioning as first intermediate hosts (Théodoridès 1989; Marcogliese 1995; Esch et al. 2002; Galaktionov and Dobrovolskij 2003; Bullard and Overstreet 2008). By contrast, less work has been done on epibionts and parasites interacting with holoplanktonic mollusks (an artificial assemblage of several subgroups of gastropods that spend their entire life in the water column, commonly referred to as pteropods and heteropods). Holoplanktonic mollusks include about 250 species, most of them with worldwide geographic

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distribution inhabiting tropical and subtropical latitudes in the Atlantic, Pacific, and Indian oceans (Lalli and Gilmer 1989; Richter and Seapy 1999; van der Spoel and Dadon 1999; Batistić et al. 2004; Moreno-Alcántara et al. 2014). Besides such characteristics, their population dynamics, vertical migration patterns (primarily epipelagic), and trophic interactions make these snails well-suited to serve as model to investigate them as vectors of agents causing diseases (White 1977); MacLean et al. 1981) or as potential hosts in life cycle of parasites and epibionts in the pelagic realm.

*Firoloida* is a monotypic genus, represented by the species *Firoloida desmarestia* Lesueur, 1817 (Gastropoda: Pterotracheidae), a medium-sized, naked pelagic heteropod with an almost completely transparent soft body and circumglobal distribution in tropical and subtropical latitudes (Lalli and Gilmer 1989; Seapy et al. 2003). This holoplanktonic mollusk may be sufficiently numerous, attaining high densities to form sonic scattering layers (Blackburn 1956). In the Gulf of California, it contributes approximately 6% of the total abundance of holoplanktonic mollusks (Angulo-Campillo 2010), whereas in neritic waters of the Gulf of México, it is relatively abundant (Taylor and Berner 1970; Seapy 1990; Lemus-Santana et al. 2014). Active swimming behavior and well-developed eyes suggest that it is a visual carnivore, which feeds mainly on gelatinous zooplankton, chaetognaths, copepods, and other holoplanktonic mollusks (Land 1982; Lemus-Santana et al. 2015). On the contrary, aside from cannibalism, *F. desmarestia* is preyed on by other heteropods, as well as fish from different trophic levels (Thiriot-Quievreux 1973; Lalli and Gilmer 1989). These predator–prey relationships may favor the dynamics of parasitic infections, especially for parasites using trophic links as a way of transmission, i.e., gregarines and helminths (Lafferty and Kuris 2002; Dobson et al. 2008). While many other zooplanktonic taxa are well known as paratenic, intermediate, or final hosts for parasites in the pelagic realm, the scant research and lack of a quantitative approach on parasites infecting holoplanktonic mollusks limits understanding of their ecological function in the life cycle of helminths or any other parasitic group (Table 1).

To date, Théodoridès (1989), Lalli and Gilmer (1989), and Marcogliese (1995) independently reviewed parasites on marine zooplankton, including holoplanktonic mollusks; however, most helminth records on pelagic snails previously published by Leuckart (1854), Bonnevie (1916), Slankis and Shevchenko (1974), MacLean et al. (1981), and Lester and Newman (1986) were overlooked. So far, nematodes, cestodes, and trematodes have been recorded infecting at least six families of holoplanktonic mollusks: the pteropods Cavoliniidae Gray, 1850 (1815), Cliidae Jeffreys, 1869 and Cuvierinidae van der Spoel, 1967, and the heteropods Atlantidae Rang, 1829, Carinariidae Blainville, 1818, and Pterotracheidae Rafinesque, 1814. However, some of those records have not been formally published. Remarkably, except

for Lester and Newman (1986), who described Hemiuroidea rediae (superfamily level), the remaining helminth records lack description or they have been incipiently described to phylum or order level (Table 1).

In this work, we carried out the first quantitative study of trematode parasitic interaction on *Firoloida desmarestia*, providing estimates on abundance of both parasites and *F. desmarestia* parasitized in the water column collected during two sampling campaigns, one in the Eastern Pacific Ocean and the other in the Gulf of California. Trematodes rediae and metacercariae belonging to two distinct superfamilies are described and we provide the first identification of a helminth species (*Opechona pyriformis* (Linton, 1900) Bray & Gibson, 1990) infecting a holoplanktonic mollusk host. New insights on the ecological role of *F. desmarestia* in the pelagic life cycle of digeneans are proposed in a conceptual model, and the implications of infection by trematodes within same *F. desmarestia* swarm are discussed.

## Material and methods

A total of 97 quantitative zooplankton samples were collected within the epipelagic zone during two sampling campaigns in March 2012 in the Eastern Pacific Ocean (Fig. 1a,b). The first survey consisted on 83 sampling stations from a cruise on the Mexican RV Francisco de Ulloa off the Baja California Peninsula by the Mexican Investigation of the California Current program (IMECOCAL), using standard bongo net trawls (500  $\mu$ m mesh) equipped with a digital flowmeter. Another 14 standard planktonic superficial samples were taken at La Sorpresa Beach, Gulf of California (24° 15' 1" N, 110° 9' 37" W), using a 500- $\mu$ m mesh net with an attached flowmeter. In both sampling areas, zooplankton samples were fixed in the field with 4% formalin buffered with a saturated sodium borate solution (Smith and Richardson 1979). In the laboratory, holoplanktonic mollusks were sorted from the zooplankton samples without fractioning. *Firoloida desmarestia* specimens were identified and sexed according to Seapy (2008). Station abundance of *F. desmarestia* was standardized according to the volume of filtered water to ind. 1000 m<sup>-3</sup> (Smith and Richardson 1979).

Taxonomic identification of the parasites in redia and metacercarial stage used specialized taxonomic references (Køie 1975; Lester and Newman 1986; Stunkard 1969, 1980; Gómez del Prado-Rosas et al. 2000). Parasite specimens were dissected from the infected heteropods with acupuncture needles, stained in Harris hematoxylin, and temporarily and/or permanently mounted. Parasite measurements were made with an Olympus Bx43 microscope equipped with a calibrated micrometer. Two dissected rediae and four metacercaria specimens were used for scanning electron microscopy (SEM) examination. They were processed through an alcohol dehydration series, dried with a critical point dryer, and mounted

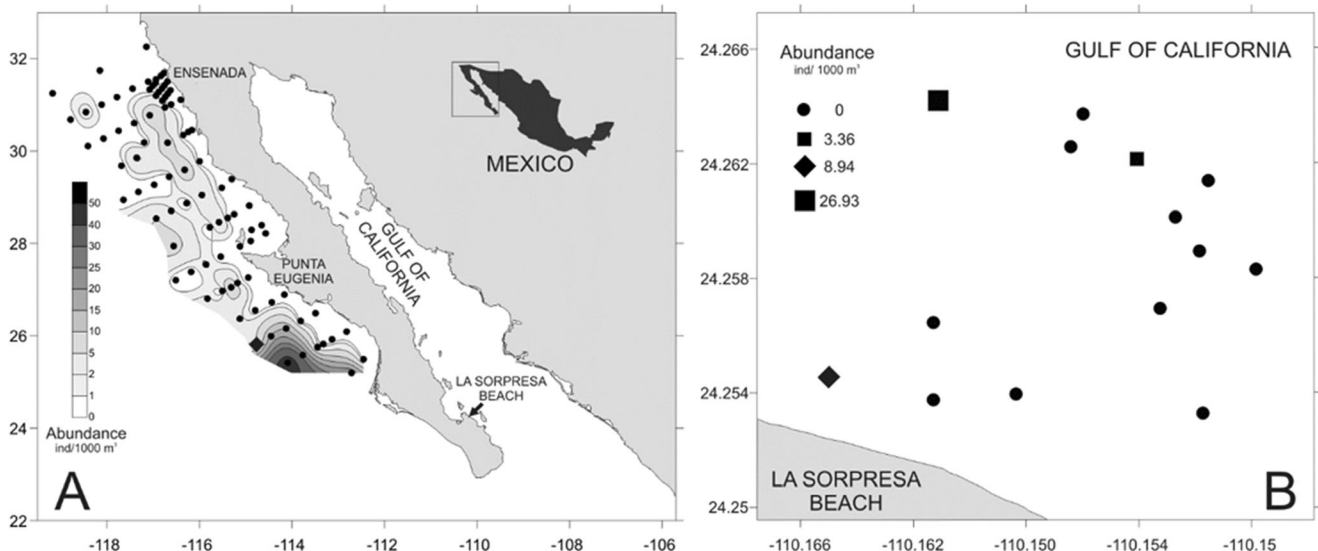
**Table 1** Helminth infection records on holoplanktonic mollusks

Host	Parasite			Region		Reference
	Species	N	Taxa	Stage	Microhabitat	
Atlantidae	<i>Atlanta</i> sp. Lesueur, 1817		Nematoda (Ne)			<sup>a</sup> Hochberg and Seapy (1985)
Carnariidae	<i>Carinaria</i> sp. Lamarck, 1801		Trematoda (Tr)			<sup>a</sup> Hochberg and Seapy (1985)
Pterotracheidae	<i>Firolida desmarestia</i> Lesueur, 1817		Digenea (Distomum) (Tr)		Endoparasitizing	Leuckart (1854)
	<i>F. desmarestia</i>		Digenea (Tr)			<sup>a</sup> Hochberg and Seapy (1985)
	<i>F. desmarestia</i>	316	Hemiuroidea (Tr)	Redia, cercaria	Hemocoel	Lester and Newman (1986), Newman (1990)
	<i>F. desmarestia</i>	15	<i>Opechona pyriformis</i> (Tr)	Metacercaria	External body, between the epithelium and muscle layer and hemocoel	Present work
	<i>F. desmarestia</i>	100	Hemiuroidei (Tr)	Redia, cercarial body	Hemocoel	Present work
	<i>Pterotrachea hippocampus</i> (= <i>Firola frederica</i> ) Philippi, 1836		Digenea (Distomum) (Tr)		Endoparasitizing	Leuckart (1854)
Unknown	<i>Pterotrachea</i> sp. unknown	9	Digenea (Tr) Cestoda (Ce)	Plerocercoid	Digestive diverticula	<sup>a</sup> Hochberg and Seapy (1985) <sup>b</sup> MacLean et al. (1981)
Cavolimiidae	<i>Diacavolinia longirostris</i> (Blainville, 1821) (= <i>Cavolina longirostris</i> )	22	Cystophorous cercaria (Tr)	Redia, cercarial body	Endoparasitizing	Vande-Vusse (1980)
Ciliidae	<i>Clio pyramidata</i> Linnaeus, 1767 (= <i>Euclio pyramidata</i> )	1	Trypanorhyncha (Ce)	Metacystode		Slankis and Shevchenko (1974) Théodorides (1989)
Cuvierinidae	<i>Cuvierina columnella</i> (Rang, 1827)		Digenea (Ce)	Redia	Hermaphroditic gland	Bonnevie (1916)

Number of analyzed hosts (N), prevalence is given in percentage (P), intensity of infection (I), cestode (Ce), Trematode (Tr), nematode (Ne)

<sup>a</sup> This is a symposium work cited in Lalli and Gilmer (1989)

<sup>b</sup> More likely tetraphyllidean plerocercoid (JRMA, personal observation)



**Fig. 1** Study area with distribution and abundance of *Firoloidea desmarestia*. **a** Mexican Investigation of the California Current program (IMECOCAL). **b** La Sorpresa Beach, Gulf of California. Black circles indicate sampling stations and black diamond shows the occurrence of parasitized host

with a double-sided adhesive carbon tape onto SEM stubs. The stubs were coated with gold-palladium (Polaron E5100) in an argon atmosphere and examined under a Hitachi S-3000N scanning electron microscope at 25 kV. External surface ultrastructure and internal description of rediae was carried out with the fracturing technique, while whole metacercaria specimens were used for description. Measurements of range, mean, and standard deviation (when possible) are given in micrometers, unless otherwise indicated.

The infection was ecologically characterized with estimates of prevalence (number of hosts parasitized with a parasite species divided by the number of host specimens examined, expressed in percent) and intensity (number of individuals of a parasite species detected on each parasitized host) (Bush et al. 1997). Abundance of trematode-infected *F. desmarestia* was standardized to ind. 1000 m<sup>-3</sup> to estimate population abundance (PA) of parasites in the sampled water column (Smith and Richardson 1979; Morales-Ávila et al. 2015). The Mann-Whitney *U* nonparametric test was used to compare outcomes between male and female size.

## Results

### Abundance, sex, and body size of hosts

*Firoloidea desmarestia* specimens were recovered ( $n = 115$ ) in both sampling areas. In the IMECOCAL cruise, they occurred at 25 of 83 sampling stations ( $n = 100$ ) with range density from 2 to 50 ind. 1000 m<sup>-3</sup>. Although this species was present at oceanic (> 1000 m seafloor depth) and coastal stations, higher abundance was observed at oceanic stations, mainly in the southern portion of the sampling grid (Baja California Peninsula) (Fig. 1a). In

contrast, at La Sorpresa Beach, this pelagic snail occurred only in three sampling sites (March 2012;  $n = 15$ ) with interval density ranging from 3 to 27 ind. 1000 m<sup>-3</sup> (Fig. 1b).

Females were more abundant and significantly larger than males in both sampling areas, sex ratio 1.5:1, and mean total length 25.4 and 21.3 mm in IMECOCAL, and sex ratio 2.7:1, mean total length 19, and 16.2 at La Sorpresa (Wilcoxon-Mann-Whitney *U* test,  $P < 0.05$ ).

### Characterization of the infection—first intermediate host

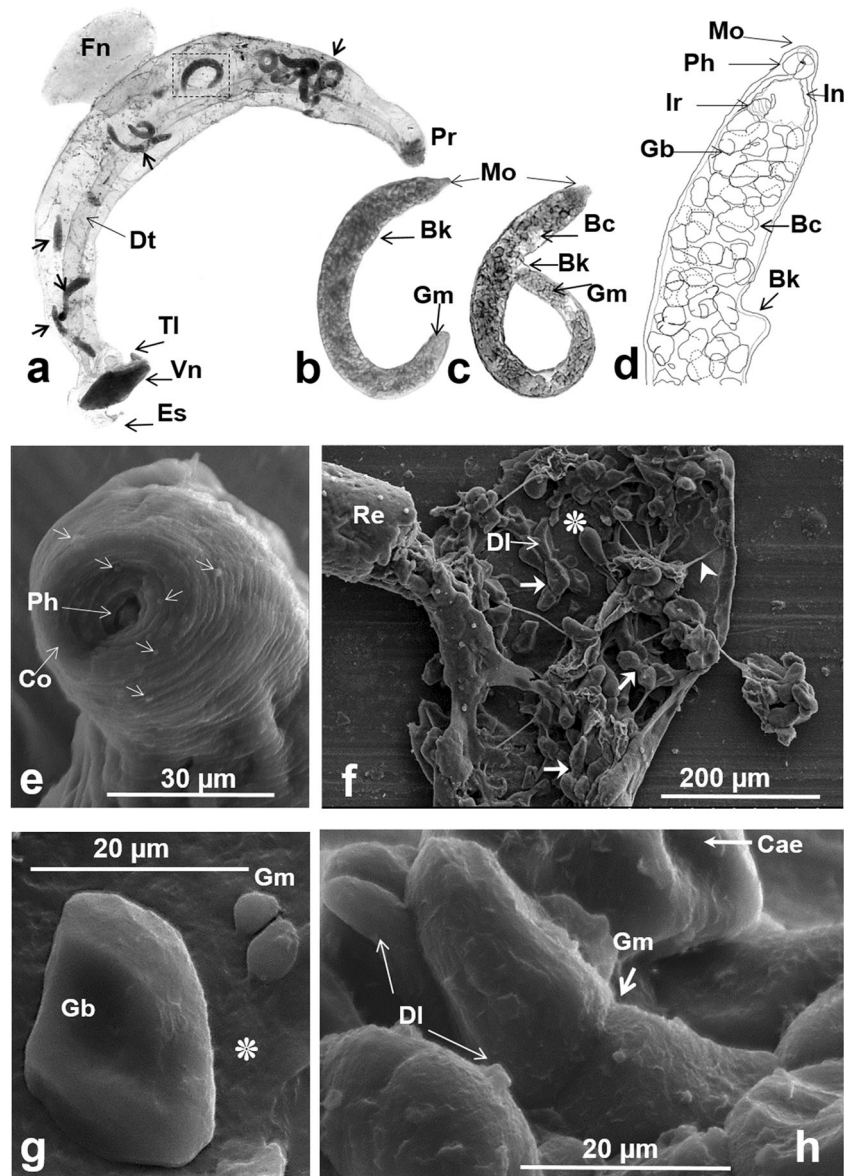
Rediae stages of trematodes (superfamily Hemiuroidae) containing intra-redial cercariae were recovered from *F. desmarestia* in the IMECOCAL cruise samples. Rediae infected only one female (out of 62) at an oceanic station (3486 m seafloor depth) 130.45 (25° 59' 359" N, 114° 27' 101" W) (Fig. 1a). Rediae occurred internally, infecting the muscle layer (hemocoel) of the host (13.8 mm total length) with prevalence of 1%, although sampling station prevalence was as high as 14% and intensity of 11 rediae per host. Abundance estimates of *F. desmarestia* infected with rediae showed up to 2.1 infected host 1000 m<sup>-3</sup> (Fig. 2a–d), whereas hemiuroid rediae density was estimated as high as 23 ind. 1000 m<sup>-3</sup>.

### Characterization of infection—second intermediate host

Young unencysted metacercariae stages of *Opechona pyriformis* (Lepocreadiidae) parasitized one *F. desmarestia* female (11.1 mm total length) caught at La Sorpresa Beach (March 2012) (Fig. 1b). These trematodes infected *F. desmarestia* with prevalence of 6.6%. However, sampling



**Fig. 2** *Firoloida desmarestia* as first intermediate host. **a** *F. desmarestia* female infected with Hemiuroidea rediae. **b** Microphotographs of two dissected rediae. **c** Hemiuroidea redia dissected from *F. desmarestia* (see dotted square in **a**). **d** Drawing of the redia showing intraredial stage. **e** Anterior end of the parthenita redia showing detail of terminal birth pore and pharynx (Ph) with unciliated sensory papillae (arrows). **f** Brood chamber of redia (\*) showing internal muscular fibers (arrowhead) and developing cercariae (arrows), note different levels of swelling in tails. **g** Germinal mass and development of germinal balls in division phase. **h** Posterior end of redia brood chamber showing germinal balls. Brood chamber (Bc), Bulk (bud-like projection) (Bk), Collar (Co), Concave anterior end (Cae), Delivery tube in formation (DI), Digestive tube (Dt), Egg string (Es), Fin (Fn), Intestine (In), Intraredial stage (Ir). Mouth (Mo), Germinal mass (Gm), Germinal balls (Gb), Redia (Re), Visceral nucleus (Vn)



station prevalence was observed as high as 33% and intensity of nine trematodes. Abundance of *F. desmarestia* parasitized with *O. pyriformis* is estimated up to 2.3 infected host 1000 m<sup>-3</sup> (Fig. 2a–d), whereas density of *O. pyriformis* was as high as 25 ind. 1000 m<sup>-3</sup>.

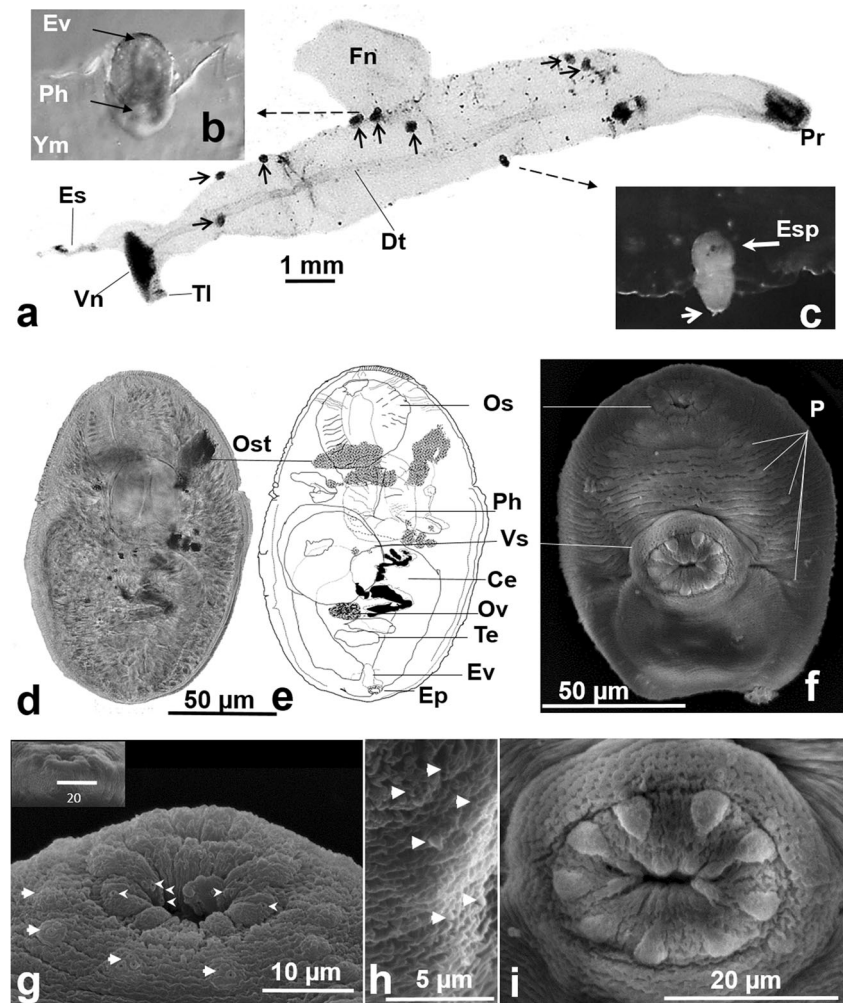
*O. pyriformis* infects *F. desmarestia* by penetration, which occurred in four microhabitats of the same host: (a) externally attached on the body ( $n = 2$ ); (b) in the penetration process on the epithelium of the host ( $n = 2$ ); (c) embedded between the epithelium and the muscle layer ( $n = 2$ ), and (d) in the muscle layer (haemocoel) ( $n = 3$ ) (Fig. 3a–c).

### Parasite diagnosis—redia

Worm-shaped body, without appendages, elongated, and cylindrical with pointed anterior end (Fig. 2a–d). Size varied

considerably 1.31–2.31 ( $1.83 \pm 0.36$ ,  $n = 11$ ) mm total length, and 0.12–0.75 ( $0.25 \pm 0.17$ ,  $n = 11$ ) mm total width. Birth pore terminal and most likely projectable, located at the anterior end 26.1–31.2 ( $28.8 \pm 2.1$ ,  $n = 4$ ) with unciliated sensory papillae spread around it (Fig. 2e). Pharynx 6.9–12.0 ( $9 \pm 2.1$ ,  $n = 4$ ) with rounded muscular walls and rudimentary intestine (sac-like caecum) (Fig. 2d). Collar inconspicuous (Fig. 2e). A process (bud-like projection) present at anterior one third of the body (Fig. 2b–d). Brood chamber of each redia was filled mostly with less-developed germ cells (at posterior region) 4.5–10.6 ( $8.2 \pm 1.8$ ,  $n = 15$ ) diameter (Fig. 2b–d, f), which are at first, a subspherical mass of dividing cells by a transverse constriction into two parts (Fig. 2f–h). The most-developed germ cells (called cercarial bodies) 22.6–37.9 ( $29.9 \pm 4.4$ ,  $n = 14$ ) in diameter were located mainly at the anterior region of the body near the mouth toward the birth

**Fig. 3** *Firoloida desmarestia* as second intermediate host. **a** *F. desmarestia* female infected with young unencysted metacercarial stage of *Opechona pyriformis* (arrowhead). **b** Young metacercaria of *O. pyriformis* penetrating into the hemocoel at the base of *F. desmarestia* fin. **c** Young metacercaria in penetration process through epithelium, arrow shows ocellar stain at anterior body of the trematode (embedded into the host). **d** Photomicrograph of *O. pyriformis* young unencysted metacercaria dissected from *F. desmarestia*, stained with Harris hematoxylin. **e** *O. pyriformis* drawing. **f** Image (scanning electron microscope) showing the whole body. **g** Apical view of oral sucker showing ten domed unciliated papillae. **h** Spinous tegument. **i** Ventral sucker (acetabulum) showing nine domed unciliated papillae on its rim. Cecum (Ce), Digestive tube (Dt), Egg string (Es), Excretory vesicle (Ev), Excretory pore (Ep), Eyespot (Es), Fin (Fn), Oral sucker (Os), Ocellar stain (Ost), Ovary (Ov), Pharynx (Ph), Proboscis (Pr), Testicles (Te), Ventral sucker (Vs), Ventrolateral papilla (P), Visceral nucleus (Vn)



pore of the redia (Fig. 2b–e). Intraredial germ cells (no trichocercous) are typically concave at one end (side most likely developing into the delivery tube, after expulsion from redia) (Fig. 2h).

**Remarks:** Rediae containing intra-redial cercariae were located predominantly free in the hemocoel of *F. desmarestia*. Although, presumably, rediae found here are not completely developed, their characteristics are similar to specimens found infecting the same host species in Carpenteria, Australia (Lester and Newman 1986). These authors did not identify the rediae; they suggested that rediae more likely belong to the superfamily Hemiuroidea. However, as we did not observe extra-redial cercariae (more developed individuals), based on external and internal morphology of rediae and some intrarediae, we assigned these to the superfamily Hemiuroidea.

#### Parasite diagnosis—young unencysted metacercariae

*Opechona pyriformis*, oval-shaped body 117–134 ( $125.5 \pm 6$ ,  $n = 4$ ) total length and 83–107 ( $98 \pm 13$ ,  $n = 4$ ) width

(maximum body width, near the level of the acetabulum) (Fig. 3). Single-pointed tegumental spines 0.67–1.32 ( $0.92 \pm 0.2$ ,  $n = 30$ ) long and 0.5–0.83 ( $0.65 \pm 0.12$ ,  $n = 30$ ) width at base (Fig. 3h). Eyespot pigment present between the oral sucker and the pharynx (Fig. 3c–f). Oral sucker subterminal 19.2–44 ( $33.8 \pm 10$ ,  $n = 4$ ) total length and 24.7–43 ( $34.7 \pm 7.6$ ,  $n = 4$ ) width. Ten domed unciliated papillae on the oral sucker lip, which contains 1–4 uni-ciliated papillae each (Fig. 3f, g). Pre-pharynx, esophagus, or pseudo-esophagus not observed (due to contracted specimen, Fig. 3f). Pharynx 31–34 ( $32 \pm 2$ ,  $n = 4$ ) long and 26–28 ( $27 \pm 1$ ,  $n = 4$ ) width. Acetabulum 37.6–39 ( $38.7 \pm 0.7$ ,  $n = 4$ ) long and 39–40 ( $41 \pm 3$ ,  $n = 4$ ) wide. Nine domed unciliated papillae on its rim (Fig. 3f, i) and some uni-ciliated papillae present on the internal rim (Fig. 3f). Caecal bifurcation anterior to the acetabulum. Intestinal caeca lateral, which join the excretory vesicle (I-shaped) to form the uoproct. Two testes, tandem at posterior third of the body (Fig. 3d, e). Excretory pore is at the end of the body.

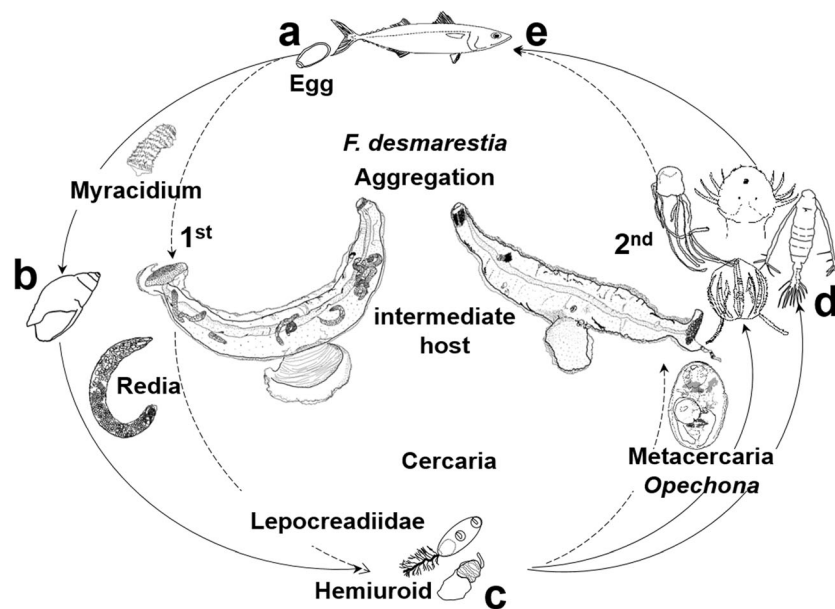
**Remarks:** The genus *Opechona* Looss, 1907 is commonly recorded infecting gelatinous zooplankton, as well as soft-

bodied chaetognaths (Gómez del Prado-Rosas et al. 2000; Júnior et al. 2013; Lozano-Cobo et al. 2017). Internal and external characteristics of young unencysted metacercariae found in our study concur with specimens previously described of parasitizing gelatinous zooplankton *Eirene lactea* (Hydrozoa) in the Caribbean Sea (Gómez del Prado-Rosas et al. 2000). *Opechona pyriformis* infecting *F. desmarestia* represents the first trematode species known to infect a holoplanktonic mollusk as a second intermediate host.

## Discussion

The scarce information on helminth parasites infecting holoplanktonic mollusks is fragmented, with few species understudied. From the records, so far, the trematoda is the only helminth group infecting the family Pterotracheidae (*Pterotrachea* and *Firoloida*). In this work, we showed that *F. desmarestia* interacts with different developmental stages of trematodes, which reveals new insights of its function as host for this parasitic group (Fig. 4(a–e), Table 1). The pelagic snail *Firoloida desmarestia* functions as a suitable first intermediate host harboring Hemiuroidea parthenita rediae, which contain developing intra-redial cercariae stages. This shows that asexual reproduction of rediae occurs in *F. desmarestia*. Thus, it is expected that more than one generation of rediae may occur

infecting the same host (Stunkard 1969; Køie 1975). As part of the ongoing infection, each redia expels cercariae into the hemocoel of the same *F. desmarestia*, as previously observed by Lester and Newman (1986). Although we did not find extra-redial cercarial stages freed in the hemocoel of the host (but in the rediae), according to Køie (1975), finding of rediae indicates that the infection was in the early phase of dispersion. Considering that cercariae are the free-swimming dispersive stages, as part of their life cycle (indistinctly hemiuroid or lepecreadiid), hundreds to thousands will leave the body of an infected *F. desmarestia* to parasitize (by ingestion or active penetration) a paratenic or second intermediate host (Fig. 4(c, d)). Lester and Newman (1986) mention that hemiuroid cercariae possibly escape from *F. desmarestia* through the genital pore via the permanent egg string. Likewise, hemiuroid and lepecreadiid cercariae of *Opechona bacillaris* (Molin, 1859) Dollfus, 1927 (= *Pharyngora*) have been recovered free from plankton samples, where soft-bodied organisms were infected with the same trematode species (Lebour 1917; Dawes 1958; Køie 1982). In context, the occurrence of trematodes, mostly as redia and cercaria stages infecting the genera *Cuvierina*, *Diacavolinia*, *Carinaria*, *Pterotrachea* and *Firoloida*, supports the idea that holoplanktonic mollusks play a remarkable role as first intermediate hosts (Table 1). In this way, trematodes infecting nektonic predators could spend their whole life cycle in the



**Fig. 4** a–e Conceptual model showing function of *Firoloida desmarestia* in the pelagic life cycle involving Hemiuroidea and Lepocreadiidae digeneans. Typical conceptualized digenean life cycle including a benthic/neritic first intermediate host (continued arrow) and the proposed role of *F. desmarestia* as intermediate host (pelagic life cycle) in the life cycle of these parasitic group (dotted arrow). (a) Eggs are shed to the environment with final host feces (nektonic fish). (b) The ciliated (hypothetic) larva myracidium emerges from the egg, and it is ingested or actively penetrates the first intermediate benthic/neritic or pelagic

mollusk host (*F. desmarestia*) to become sporocyst-redia. (c) Free swimming cystophora–hemiuroidea or likely trichocercous–Lepocreadiidae tailed cercaria stages passively/actively (respectively) seek for a second intermediate host (crustacean, gelatinous or soft-bodied zooplankton). (d) Second intermediate hosts harboring the trematode infective stage (metacercaria) parasitize the predatory nektonic fish (final host) throughout trophic interaction, where the trematode becomes adult and reproduce



pelagic realm, i.e., without infecting benthic mollusk first intermediate hosts (Fig. 4(a–e)) (Leuckart 1854; Bonnevie 1916; Vande-Vusse 1980; Hochberg and Seapy 1985; Lester and Newman 1986). This perspective substantially modifies previous conceptualizations that holoplankton functions only as paratenic or second intermediate hosts in life cycles of digenetic trematodes infecting pelagic fish (Théodoridès 1989; Marcogliese 1995). Besides, finding rediae infecting *F. desmarestia* at oceanic and coastal stations, as observed in other holoplanktonic mollusks (Leuckart 1854; Bonnevie 1916; Vande-Vusse 1980; Hochberg and Seapy 1985; Lester and Newman 1986) shows the relevance of holoplanktonic mollusks in the dynamics of transmission of trematodes by dispersing cercariae to infect other planktonic groups (Fig. 4(b–d)). So far, hemiuroid redia containing cystophorous cercariae (characterized by the presence of a lumen or cyst between the tail and body, into which the whole body is invaginated and equipped with a delivery tube) of unknown species are the only trematodes known to infect holoplanktonic mollusks (Vande-Vusse 1980; Lester and Newman 1986). Nevertheless, it is likely that some of them belong to distinct taxonomic groups, since the families Bivesiculidae, Azygiidae, Hirudinellidae, Bathycotylidae, Gorgoderidae, Hemiuridae, Didymozoidae, and Lecithasteridae are reported to produce cystophoric cercariae sensu lato (Pearson 1992; Martorelli 1994; Køie 1995; Køie et al. 2002). So far, scarce published information shows that helminth infection research in holoplanktonic mollusks is rather neglected (Table 1). In addition, it is difficult to correlate these developmental stages with adult (mature) specimens, making species of their parasite richness and abundance underestimated.

On the other hand, finding of young unencysted metacercariae in four microhabitats of the same host show that *O. pyriformis* infects *F. desmarestia* by active penetration, i.e., after cercariae emerged from the first intermediate host and freed into the water column. This finding concurs with results reported by Stunkard (1969) and Køie (1975), who showed that, under laboratory conditions, *O. pyriformis* (= *Neopechona pyriforme*) and *O. bacilliaris* infected gelatinous and soft-bodied planktonic hosts by the same mode. Likewise, occurrence of larval stages of *O. pyriformis* suggests that this parasite changes ontogenetically in the host, supporting that *F. desmarestia* functions as a second intermediate host in the transmission of *O. pyriformis* to higher trophic levels (through predator–prey relationships). This is the first record of *F. desmarestia* functioning as a second intermediate host harboring metacercaria stages of trematodes. Estimates of prevalence, intensity, and parasite abundance, as well as density of *O. pyriformis*-parasitized hosts, represent the highest prevalence value reported so far on trematodes infecting *F. desmarestia* (see Table 1). The genus *Opechona* naturally infects gelatinous and soft-bodied zooplankton,

reaching high prevalence values from the Atlantic, Pacific, and Indian Oceans, and the Caribbean and Gulf of Mexico (Reimer et al. 1971; Martorelli 1996, 2001; Gómez del Prado-Rosas et al. 2000; Øresland and Bray 2005; Morandini et al. 2005; Daponte et al. 2006, 2008; Nogueira-Júnior et al. 2013, 2015; Martell-Hernández et al. 2011; Kondo et al. 2016).

So far, it is well documented that freshwater and marine snails serve as intermediate hosts for numerous species of larval trematodes. So, it is expected that any population of snails may be infected by several species of parasites, sometimes as a mixed infection (Stunkard 1980; Sousa 1992). For instance, rediae of the families Hemiuridae, Opecoleidae, and Lepocreadiidae have been recorded parasitizing snails of the genera *Buccinanops*, *Conus*, *Nassarius*, and *Annarchis* (Køie 1975; Stunkard 1980; Averbuj and Cremonte 2010; Barnett et al. 2014). In contrast, although in holoplanktonic mollusks occurrence of redia stages is poorly known, metacercariae stages of Hemiuridae and Lepocreadiidae have been commonly reported infecting the same species of gelatinous and soft-bodied zooplankton (Yip 1984; Jarling and Kapp 1985; Martorelli 2001; Daponte et al. 2006; Briz et al. 2012; Lozano-Cobo et al. 2017). In our study, we showed that *F. desmarestia*, a soft-bodied pelagic heteropod, has functions as a host harboring separately both rediae and metacercariae, evidently belonging to different superfamilies. Based on this, we hypothesize that, since *F. desmarestia* functions as a source of infection (by releasing/dispersing cercariae) to other zooplanktonic groups, it is also likely that, during this transmission event, some individuals of *F. desmarestia* of the same swarm might acquire the infection, which in turn could host metacercariae of the same trematode species (Fig. 4(b–d)). From this perspective, development of redia, cercaria, and metacercaria stages might occur infecting different individuals of the same host species. Although, the typical three-host life cycle would also be maintained in these trematodes, the number of species used as a first and second intermediate host could be significantly shortened. Poulin and Cribb (2002) showed that, one way to shorten the life cycle occurs when trematodes use their first intermediate host as a second intermediate host (see their Fig. 1(c)). However, these authors assert that, in that kind of truncation, the parasite never abandons its first intermediate host. Although, shorter life cycles may be adopted by all members of a species, in some cases, it appears to be a facultative developmental strategy, only seen in certain individuals of a species (Poulin and Cribb 2002). Thus, both the three-host cycle and the abbreviated cycle might be displayed by conspecific worms. Trematodes of the superfamily Hemiuroidea are reported to shorten its life cycle by developing sexual adults in first intermediate host (Jamieson 1966), while the family Lepocreadiidae exhibits facultative progenesis in the second intermediate host (Macfarlane 1951). Regarding this, more research is needed in the



*F. desmarestia*–trematode interaction to elucidate first, the trematode diversity of both rediae and metacercaria stages, and second, if truncation of the life cycle (hypothesized in our study) could result in a variant of the kind discussed in Poulin and Cribb (2002).

This is the first quantitative study regarding helminth infection in *Firoloidea desmarestia*. This heteropod (pelagic snail) showed a dual host function in the life cycle of trematodes, acting as a first intermediate host for rediae (hemiurid) and alternatively as a second intermediate host for metacercariae of *Opechona pyriformis*. Occurrence of the latter showed that *F. desmarestia* interacts with a more diverse parasitic assemblage than previously thought. Overall, this heteropod potentially transmits parasites to two distinct trophic levels, infecting not only zooplankton, but also nektonic predators (more likely Scombrids fish) in both oceanic and coastal zones. Estimates of infection levels and dual host functions support the relevance of *F. desmarestia* as a remarkable host in transmission dynamics, so that digeneans can spend their whole life cycle infecting only pelagic hosts.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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